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GENERIC STATUS OF THE  
INOCERAMUS? TEGULATUS  
SPECIES GROUP (BIVALVIA) OF  
THE LATEST CRETACEOUS OF  
NORTH AMERICA AND EUROPE

IAN G. SPEDEN







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GENERIC STATUS OF THE *INOCERAMUS? TEGULATUS* SPECIES GROUP (BIVALVIA) OF THE LATEST CRETACEOUS OF NORTH AMERICA AND EUROPE

IAN G. SPEDEN

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(Received February 3, 1969)

ABSTRACT

Five named species of the latest Cretaceous *Inoceramus? tegulatus* species group are, on present information, considered valid: two from North America, *fibrosus* (Meek and Hayden) and *argenteus* Conrad; three from Europe, *tegulatus* Hagenow, *caucasicus* Dobrov and *dobrovi* Jeletzky. The morphology of the ligament area and the pattern of muscle scars differentiate the species from *Inoceramus*, and *Tenuipteria* Stephenson is the valid generic name for the broad taxon encompassing the five species.

The five species can be divided into two lineages: a lineage of equivalved species (*tegulatus*, *fibrosus*, *caucasicus*) and a lineage of inequivalved species (*argenteus*, *dobrovi*). The equivalved species occur in the uppermost Late Campanian, Early Maestrichtian and lowermost Late Maestrichtian, and the inequivalved species appear to be restricted to the Late Maestrichtian.

*Tenuipteria fibrosa* and *argentea* are redescribed and illustrated, a neotype for *argentea* is designated, and a lectotype for *T. tegulata* is designated.

## INTRODUCTION

Externally similar species of *Inoceramus*?, characterized by relatively strong concentric and radial plicae, occur in the latest Campanian and Maestrichtian of Europe and North America. These species are included by authors in a single species group, that of *Inoceramus? tegulatus* Hagenow (Jeletzky and Clemens, 1965). The stratigraphic range in regions of Europe and North America of the five species here accepted as valid is given in Figures 1 and 2.

Species included in this group are frequently referred to in biostratigraphic studies and in discussions of inter-regional correlations among North America, Western Europe and Russia (Dobrov, 1951; Seitz, 1959; Jeletzky, 1962). However, because of a lack of knowledge of internal morphology, the generic position of *I.? fibrosus* (Meek and Hayden) and the other species has been uncertain (Jeletzky, 1962, p. 1014; Jeletzky and Clemens, 1965).

Well-preserved specimens of *I.? fibrosus* from the Mobridge Member of the Pierre Shale and the overlying Fox Hills Formation in the type area of the latter in north-central South Dakota, Western Interior of the United States (Waage, 1961, 1968), provide for the first time full details of the hinge morphology and musculature of the species. These data, together with similar data for two other members of the species group, *I.? tegulatus* Hagenow from Europe and *Tenuipteria argentea* (Conrad; Stephenson, 1955) from the Owl Creek Formation, Gulf Coast, North America, permit a reevaluation of the generic status of these species.

Abbreviations used in the text and plate captions are:

- |         |  |
|---------|--|
| MMH     | — Mineralogisk-Geologiske Institut, Copenhagen, type specimen number       |
| NZGS-WM | — New Zealand Geological Survey, World Mollusca Collection                 |
| UMMP    | — University of Michigan Museum of Paleontology                            |
| USGS    | — United States Geological Survey  |
| USNM    | — United States National Museum  |
| YPM     | — Peabody Museum of Natural History, Yale University, type specimen number |
| YPM-A   | — Peabody Museum of Natural History, Yale University, collection number    |



## ACKNOWLEDGEMENTS

Comparison of the species of the *Inoceramus? tegulatus* species group was facilitated through the loan of specimens, provision of information and discussions by the following persons whose assistance is appreciated and gratefully acknowledged: Dr. Erle G. Kauffman, United States National Museum; Prof. K. M. Waage, Peabody Museum of Natural History, Yale University; Dr. J. A. Jeletzky, Geological Survey of Canada; Dr. L. B. Kellum, Museum of Paleontology, University of Michigan; Dr. Tové Birkelund, Mineralogisk Museum, Universitetets Mineralogisk-Geologiske Institut, Copenhagen; and Prof. Dr. O. Seitz and Dr. F. Schmid, Niedersächsisches Landesamt für Bodenforschung, Hannover. S. N. Beatus took most of the photographs for the plates. Drs. A. Wodzicki and G. A. Challis, New Zealand Geological Survey, kindly translated parts of Polish and Russian papers.

Drs. Kauffman, Waage, Birkelund, and G. R. Stevens and C. A. Fleming, New Zealand Geological Survey, read the manuscript and made valuable suggestions.

Specimens of *Inoceramus? fibrosa* were collected and described as part of a dissertation for the degree of Doctor of Philosophy at Yale University while the author was on leave from the New Zealand Geological Survey under a New Zealand Department of Scientific and Industrial Research National Research Fellowship.

## THE INOCERAMUS? TEGULATUS HAGENOW SPECIES GROUP

## NORTH AMERICAN SPECIES

Two groups of thin-shelled *Inoceramus?* with weak to moderately strong radial and concentric ornament have been recognized in latest Cretaceous sequences of the United States: (a) Equivalved or possibly subequivalved species with moderately inflated and weakly projecting, anteriorly situated umbones. (b) Inequivalved species with a strongly inflated left valve possessing a projecting, swollen umbone and a flattish right valve with a very slightly projecting umbone.

Three names have been given to species classified in the equivalved group. All are known only from the Western Interior.

1. *Inoceramus fibrosus* (Meek and Hayden, 1856a). Lectotype,

by subsequent designation of Meek (1876, Pl. 17, fig. 17a), USNM 460, a steinkern of a right valve, oblique length 34.7 mm. Type locality: Forks of the Cheyenne River, South Dakota. Stratigraphic position: Pierre Shale, Early Maestrichtian.

2. *Inoceramus whitii* Toepelman (1922, p. 63). Location of type material unknown (see Cobban, in Jeletzky and Clemens, 1965, p. 958). Type locality: White River Badlands, South Dakota. Stratigraphic position: from the "transitional beds between the Pierre and Fox Hills" (Toepelman, 1922, p. 63), Early Maestrichtian.

Jeletzky (Jeletzky and Clemens, 1965) thought that this interval might be equivalent to part of the Mobridge Member, at the top of the Pierre Shale, in the Missouri Valley succession, but it could in part be equivalent to even older Pierre Shale units (Waage, 1961, 1968).

3. *Inoceramus cobbani* Kellum (1964, p. 1006; = *radiatus* Kellum, 1962, *non* Heine, 1929). Holotype, the original (and only) specimen of Kellum (1962, Pl. 3, fig. 17), UMMP 37433, a left valve, length 22.9 mm. Type locality: 1924/K-6, Old Woman Creek, Niobrara County, Wyoming. Stratigraphic position: Fox Hills Sandstone, Maestrichtian.

In addition to these three named "species" Cobban (1964, p. A136) has recognized a stratigraphic succession of four forms, each with a different pattern of ornament:

... an early form with weak radial and concentric folds, a later form (typical form) in which radial folds dominate over the concentric ones, and a still later form in which radial and concentric sculpture is of about equal strength, and a final form in which the concentric sculpture dominates.

The typical form of *I.?* *fibrosus* is rhomboidal in shape, has strong radial plicae and corresponds to the second group of Cobban (1964). *Inoceramus cobbani* Kellum is characterized by extremely weak radial ornament and stronger concentric plicae, and could be classed in Cobban's group four.

Jeletzky, in one of his important studies of the North American species of the *I.?* *tegulatus* species group (Jeletzky and Clemens, 1965, p. 958), noted that "representatives of *I. whitii* always occur in association and appear to intergrade with the more typical representatives of *Inoceramus?* *tegulatus*" (= *fibrosus*, according to Jeletzky). He considered *whitii* to be an extreme morphological vari-



ant of the one "polytypic species". Jeletzky also placed *cobbani* (= *radiatus*) in synonymy with *whitii*.

Populations of *I.?* *fibrosus* from all biostratigraphic zones of the Fox Hills Formation in its type area are extremely variable in shape and ornament. Individual specimens from populations of *fibrosus* match exactly the specimen of *cobbani* figured by Kellum (1962, Pl. 3, fig. 17). The same applies to *whitii* which, on the basis of Toepelman's description, is indistinguishable from the Fox Hills species. Specimens with strong radial ornament (*fibrosus* sensu stricto) occur in populations from all stratigraphic zones in the Fox Hills Formation but are more common in the underlying Mobridge Member of the Pierre Shale.

Future detailed statistically based studies on adequate samples from various horizons may prove the existence of successive subspecies. Until this type of study is undertaken the information available suggests that only one morphologically variable species, for which the name *fibrosus* has priority, should be recognized in the uppermost Cretaceous of the Western Interior of the United States and Canada. This procedure is accepted for the purpose of this paper.

Two species of inequivalved, radially plicate *Inoceramus?* have been described from the Maestrichtian of the Gulf Coast of the United States (Fig. 2).

1. *Inoceramus argenteus* Conrad (1858, p. 329). Type specimen lost (Stephenson, 1955, p. 111; Richards, 1968). Type locality: Owl Creek, Tippah County, Mississippi. Stratigraphic position: Owl Creek Formation, Maestrichtian.

2. *Inoceramus costellatus* Conrad (1858, p. 329). Other data as for *I. argenteus*.

Stephenson (1955, p. 111) synonymized *costellatus* under *argenteus* but did not discuss the reasons for this step. As Conrad described *argenteus* first on page 329, Stephenson probably used the argument of page priority. Conrad's (1858) illustrations do not permit positive conspecific identity of the two specimens. The figure of *argenteus* is poor and shows an incomplete left valve apparently marked only by fine concentric plicae. His figure of *costellatus* (1858, Pl. 34, fig. 12) is good and shows an inequivalved specimen with strong radial and concentric plicae on the right valve. Conrad recorded the presence of an inoceramid hinge on the specimen. Con-

sequently it would have been better to select *costellatus* as the valid name of the species.

Stephenson (1955) separated *argenteus* from *Inoceramus*, largely on the basis of its possession of a narrow ligament area bearing only a few (5 to 6) shallow ligament pits of irregular width, spacing and impression, and made it the type species of a new genus *Tenuipteria*. The status of this taxon is discussed in a later section.

#### EUROPEAN SPECIES

Three species and eight varieties of small, thin-shelled *Inoceramus* closely resembling *I. tegulatus* Hagenow and *fibrosus* (Meek and Hayden) have been named from latest Cretaceous sequences of an area extending from Western Europe to the Caucasus.

1. *Inoceramus tegulatus* Hagenow (1842, p. 559). Lectotype, here designated, the original of Wolansky (1932, Pl. 5, fig. 6), an almost complete left valve in the original collection studied by von Hagenow, in the Geological-Paleontological Institute, University of Griefswald, East Germany. Type locality: Rügen Island, East Germany. Stratigraphic position: Mukronatenkreide, Lower Maestrichtian (Wolansky, 1932; Nestler, 1965).

2. *Inoceramus caucasicus* Dobrov (1951, p. 167). Holotype, by original designation, specimen no. 12 of Dobrov (1951, Pl. 2, fig. 2), bivalved, height 35 mm, length of ligament area 17 mm. Type locality: Dobrun Zolka River, Northern Caucasus. Stratigraphic position: Maestrichtian (Mst. s<sub>1</sub>). (Specimen in the Geological Cabinet of Moscow State University.)

3. *Inoceramus dobrovi* Jeletzky (Jeletzky and Clemens, 1965, p. 956). Holotype, by original designation of Jeletzky (Jeletzky and Clemens, 1965, p. 956), the original of Dobrov (1951, Pl. 2, figs. 1a-c), a complete bivalved specimen, length 37 mm, height 30 mm. Type locality: Darya River, Northern Caucasus. Stratigraphic position: Maestrichtian (Mst. s<sub>2</sub>). (Specimen in the Geological Cabinet of Moscow State University.)

Dobrov (1951) also proposed eight new varieties, three under his concept of *tegulatus* Hagenow and five under his concept of *caucasicus* Dobrov, namely:

*I. tegulatus* Hagenow var. *gibbera* Dobrov

*I. tegulatus* Hagenow var. *undulato-sulcata* Dobrov

*I. tegulatus* Hagenow var. *curta* Dobrov

- I. caucasicus* Dobrov var. *monilifera* Dobrov
- I. caucasicus* Dobrov var. *cabardinica* Dobrov
- I. caucasicus* Dobrov var. *fluctuosa* Dobrov
- I. caucasicus* Dobrov var. *fistulata* Dobrov
- I. caucasicus* Dobrov var. *ravni* Dobrov

Hagenow (1842, p. 559) did not illustrate any of his specimens of *tegulatus*. A translation of his brief description follows:

6) *I. tegulatus* n. The present very damaged 10 examples allow only a general comparison to the former similar species [refers to *I. mytiloides* Mantell, a species described directly before], and both valves appear to be symmetrical and moderately strongly inflated. Just as in the case of *I. mytiloides* growth ridges are crossed by 14 to 18 radiating furrows which have a sharper base, among which 3–4 are always more prominently impressed. The generally equally broad and flat raised intervals resemble a row of overhanging flat roof-tiles with a somewhat convex front margin.

The last part of the first sentence of Hagenow's description makes it almost certain that he was studying an equivalved species. This interpretation is supported by Wolansky's (1932, p. 28–29) revision of the original collection of von Hagenow. Her statement (p. 29) "Der Angabe ödums, dass die rechte Klappe kleiner sei als die linke und keinen vorspringenden Wirbel besitze, kann ich nicht folgen, da mir auch solche Schalen mit kräftig ausgeprägtem Wirbel vorliegen" indicates a similar degree of projection of the umbones of both valves. Although Wolansky says the right valve has a strongly projecting umbone, her illustrations (Pl. 4, fig. 4; Pl. 5, figs. 5, 6), while not good, especially for the left valve, clearly show, as noted by Jeletzky (Jeletzky and Clemens, 1965, p. 956), that Hagenow's species is equivalved and has similar moderately inflated and slightly projecting umbones on each valve. Wolansky (p. 34) synonymized in *tegulatus* the specimens classified as *mytiloides* by von Hagenow.

Prior to Wolansky's (1932) restudy of Hagenow's original collection, Ødum (1922, p. 10) examined specimens from the "White Chalk of Denmark" and defined *I. tegulatus* Hagenow:

The main characteristics of *Inoceramus tegulatus* are as follows: the long anterodorsal angle, the considerable difference in convexity of the right and left valves, the radial ribs and the small ear formed by the long anterodorsal angle. To these



features may be added the absence of small pits in the ligament area. (Translation by New Zealand Department of Internal Affairs.)

In his detailed description Ødum stressed the inequivalveness and the presence of a strongly inflated and projecting umbone on the left valve and a small very weakly projecting umbone on the right valve. The few specimens and illustrations available to the writer suggest that the umbone of the right valve is less prominent than that on Hagenow's specimens (see also Jeletzky, in Jeletzky and Clemens, 1965, p. 956).

Seitz (1959, p. 123–124) was the first to point out the existence of two concepts for *I. tegulatus*: an equivalved “Avicula-like” *I. tegulatus* Hagenow (see Pl. 2, figs. 1–3) and an inequivalved “Pholadomya-like” *I. tegulatus* Hagenow of Ødum (see Pl. 2, figs. 4–6). Jeletzky (Jeletzky and Clemens, 1965) later fully documented the differences between the two species and renamed Ødum's species concept as *I. dobrovi* Jeletzky, but he selected the holotype for his new species from a suite of Caucasian specimens described and illustrated by Dobrov (1951).

Seitz also considered there to be a possible difference in ornament between *tegulatus* Hagenow and *dobrovi* Jeletzky. Specimens of the two species sent to the writer by Dr. Tové Birkelund tend to confirm Seitz' observation. *I. dobrovi* appears to have consistently finer and more regular concentric plicae and more regular radial plicae that are restricted to the anterior half of the valve, whereas the broad posterior wing has regular concentric growth lamellae only. As stressed by Seitz (1959, p. 124), additional well-preserved and accurately identified specimens are required to clarify the apparent differences in ornament and to document more adequately other possible morphological differences, especially of the form of the anterior ear of the left valve and of the ligament area of *I. dobrovi*.

Differences in the prominence of the umbone and the form of the anterior ear of valves figured by Ødum (1922) and my knowledge of these features on the North American *I. ? fibrosus* led me to suspect that Ødum may have studied specimens of both *tegulatus* Hagenow and *dobrovi* Jeletzky. My suspicion was confirmed independently by the observations of Birkelund, who commented (letter of January 15, 1966):

In Ødum's paper both *I. ? tegulatus* v. Hag. (fig. 4, 5, 6) from the Lower Maastrichtian and *I. ? dobrovi* Jeletzky (fig. 1, 2, 3, 7)

from the Upper Maastrichtian are figured. Ødum (1922) did not mention any differences between the specimens he examined from the Lower and Upper Maastrichtian of Denmark and Jeletzky (in his 1965 paper) did not realize that Ødum figured both the so-called *I.? dobrovi* and the real *I.? tegulatus* v. Hag.

The nonrecognition by Jeletzky of the mixture of species studied by Ødum does not affect in any way Jeletzky's conclusions of the validity of the two species.

The third European species, *I. caucasicus* Dobrov, was named by Dobrov during his study of the *I. tegulatus* species group in the uppermost Cretaceous of the Caucasus. Dobrov recognized two species: *I. caucasicus* in the upper Lower and lower Upper Maastrichtian (Mst. s<sub>1</sub>; upper marl) and *I. tegulatus* Hagenow in the upper Upper Maastrichtian (Mst. s<sub>2</sub>; limestone). Dobrov's text and illustrations prove conclusively that he followed Ødum's concept of *I. tegulatus*, and I agree with Jeletzky (in Jeletzky and Clemens, 1965) in accepting the *I. tegulatus* Hagenow of Dobrov as conspecific with *I. dobrovi* Jeletzky.

The varieties of *I. tegulatus* and *dobrovi* proposed by Dobrov (1951), some of which apparently occur together, are here believed to be extreme morphological variants of their respective species. *Inoceramus caucasicus* Dobrov includes specimens with strong concentrics but with very weak radials (holotype of *caucasicus*) to those with very strong radial plicae (*caucasicus* var. *fistulosa*). The latter closely resemble the holotype of *I.? fibrosus*. Specimens of *I. dobrovi* Jeletzky (= the *tegulatus* of Dobrov) show a comparable range of ornament, i.e., weak radials (*tegulatus* var. *gibbera* of Dobrov) to strong radials (*tegulatus* var. *undulato-sulcata* of Dobrov).

To summarize: As in North America, two species occur in the latest Cretaceous: an equivalved species with moderately inflated and projecting umbones, distinct anterior ears, and similar ornament on each valve (*I.? tegulatus* Hagenow), and an inequivalved species with a strongly inflated and projecting umbone on the left valve and an almost flat right valve on which the umbone barely projects above the dorsal margin (*I.? dobrovi* Jeletzky).

The problems of whether *I.? caucasicus* and *I.? tegulatus* are synonymous or distinct subspecies and the status of the varieties of Dobrov require a statistical study of stratigraphically located samples of adequate numbers of specimens, as suggested above for the North American *I.? fibrosus*. The holotype of *caucasicus* has strong con-

centrics and weak radials, whereas the lectotype of *tegulatus* has strong radial and concentric plicae. Evidence of successive populations dominated by different ornament types would favor the possibility of different subspecies or species.

Because of past confusion in the concept of the species, specimens recorded in the literature as *I. tegulatus* should be reexamined to determine whether they are *tegulatus* (sensu stricto) or *dobrovi*.

#### GENERIC POSITION OF THE SPECIES OF THE INOCERAMUS? TEGULATUS SPECIES GROUP

The generic position of the species of the *I.?* *tegulatus* species group has been uncertain from the date they were proposed, in part because of the pterioid-like shape and presence of a distinct anterior ear, largely because of our lack of knowledge of the internal morphology of the species. *Inoceramus?* *fibrosus* has been classified in *Avicula* Lamarck, *Pholadomya* G. B. Sowerby, *Pinna* Linnaeus, *Pteria* Scopoli, *Pseudoptera* Meek, *Inoceramus* J. Sowerby, *Actinoceramus* Meek, and *Tardinacara* Elias (nomen nudum) — *Inoceramus* being the most frequently used (see Jeletzky, 1962). *Inoceramus?* *tegulatus* Hagenow has been placed under *Inoceramus* and *Spyridoceramus* Heinz (1932).

*Inoceramus?* *fibrosus* (Meek and Hayden) from the type area of the Fox Hills Formation has a ligament area that is longitudinally striated, with a few irregular depressions crossing the area under the umbone, but lacking the regular incised ligament pits characteristic of *Inoceramus* (Pl. 1, figs. 1, 3). The specimens also bear a distinctive pattern of muscle scars. The true *tegulatus* Hagenow of Ødum (1922, figs. 4–6; Pl. 2, fig. 2) has a similar ligament area, but some specimens (Ødum, fig. 6) have small, faint, irregular pits along part of the ligament area similar to but less distinct and regular than those on the ligament area of species of the *I. barabini* group from the Pierre Shale (see p. 31). Dr. Birkelund (letter of February 7, 1966) has informed me that Ødum's specimen with the ligament pits is "stratigraphically older than the specimens from Alborg" which have no pits. Consequently, the degree of impression and regularity of the pits probably degenerated during the late Campanian-early Maestrichtian.

Although the musculature of *tegulatus* Hagenow is unknown, and although some doubt may exist as to the degree to which weak



ligament pits are present on the ligament area, the similarity of the ligament areas and of external morphology make it reasonably certain that *fibrosus* and *tegulatus* are congeneric. The ligament area and musculature of *caucasicus* were not observed by Dobrov. However, because of its close external similarity and approximate time equivalence with *tegulatus*, I tentatively accept *caucasicus* as congeneric with *fibrosus* and *tegulatus*.

The musculature of the inequivalved species *argenteus* Stephenson and *dobrovi* are unknown. The ligament area of *argenteus* has two to six shallow irregular pits as described by Stephenson (1955); that of *dobrovi* is unknown. Except for the inequivalveness, and the presence of irregular weak pits crossing the ligament area, *argenteus* is closely similar to *tegulatus* and *fibrosus* and is here considered congeneric with them under the broad generic diagnosis given below. Because of its close external similarity to, and approximate stratigraphic equivalence with *argenteus*, *dobrovi* is here tentatively considered congeneric with *argenteus*.

The lack of incised regular ligament pits crossing the full width of the ligament area and the presence of a distinctive pattern of muscle scars clearly separate the *tegulatus* species group from *Inoceramus* J. Sowerby, as defined by the type species *I. cuvierii* J. Sowerby (1814) (Cox, 1955).

Three names are available for the generic taxon to include *tegulatus* Hagenow, *fibrosus* (Meek and Hayden), *argenteus* Conrad, and probably the other two species also: *Tardinacara* Elias (1931, opp. p. 58, p. 122, 130), *Spyridoceramus* Heinz (1932, p. 19) and *Tenuipteria* Stephenson (1955).

*Tardinacara* was proposed by Elias (1931, p. 130) in the form "... *Inoceramus fibrosus* Meek & Hayden (*Tardinacara* [*Pseudoptera*] *fibrosa* of the writer) . . ." and was not accompanied by a diagnosis or use of the words new genus or type. As stated by Jeletzky (in Jeletzky and Clemens, 1965, p. 955) it is a nomen nudum.

*Spyridoceramus* Heinz was proposed as follows:

"*Spyridoceramus* nov. gen.

Genotyp: *Inoceramus tegulatus* HAG.

Die systematische Stellung dieser Gattung ist noch ungewiss."

There was no diagnosis, discussion or illustration, and it is not certain which concept of *I. tegulatus* Hagenow, the equivalved or inequivalved, was meant by Heinz. As Ødum's (1922) description was

relatively recent and superior to earlier descriptions, Heinz may have accepted the concept of an inequivalved *I. tegulatus* Hagenow (= *I. ? dobrovi*).

Heinz' name *Spyridoceramus* is invalid (Article 12, International Code of Zoological Nomenclature, adopted by the 15th International Zoological Congress with later minor amendments (Stoll et al., 1964)), as has been recognized by Vokes (1967, p. 171), even though Heinz selected a type species and obeyed the rules operative prior to 1931. Other workers have accepted (Aliev, 1958) or validated (Seitz, 1961) names proposed by Heinz (1932). However, as recommended by the International Commission of Zoological Nomenclature (1950, Bull. Zool. Nomenclature, v. 14, p. 563, paragraph 48), the validation of nomina nuda or invalid names may cause confusion and should be avoided.

*Tenuipteria* Stephenson 1955 is a valid name and is here applied to the five species discussed above. A diagnosis and discussion of my concept of the genus is given in the systematic section of this paper.

ADDENDUM. In the recently published Part N, Mollusca 6, Bivalvia, of the *Treatise on Invertebrate Paleontology* (R. C. Moore, ed., Geological Society of America and University of Kansas Press, 1969), a copy of which was received while this paper was in galley proof, the generic taxon *Spyridoceramus* Cox, new genus, was validated (p. N320) by the late Dr. L. R. Cox, who noted that "*Inoceramus argenteus* Conrad is the North American representative of this genus" and placed the genus in the Inoceramidae. On page N310 Cox accepted the genus *Tenuipteria* Stephenson, 1955, with *Inoceramus argenteus* as type species, and classed it in the Bakevelliidae.

If *argenteus* and *tegulatus* are considered conspecific, as clearly held by Dr. Cox and by myself in this paper, *Tenuipteria* has priority and is the valid name for the generic taxon. Future studies may permit the application of the name *Spyridoceramus* to an equivalved generic or subgeneric taxon.

## BIOSTRATIGRAPHY AND CORRELATION

### EUROPE

In Europe the species of *Tenuipteria* are recorded from the latest Campanian and Maestrichtian of the Russian Platform, northern

Poland, northern East and West Germany, Sweden and Denmark. The species are restricted to the Boreal Province (Jeletzky, 1948, 1951; Naidin, 1954; Kongiel, 1962).

Biostratigraphic subdivision of the latest Campanian and Maestrichtian of Europe has been based on many phyla and classes of organisms. Up to seven zones have been recognized in the Maestrichtian (Troelsen, 1937; see Birkelund, 1957, table 4). Belemnoids are of primary importance for zonation, and two (Naidin, 1952; Maslakova, 1959; Moskvina, 1962), three (Kongiel, 1962), four (Birkelund, 1957; Jeletzky, 1951) or five (Jeletzky, 1958, 1962; Naidin, 1960) zones are accepted.

The controversy over the identification and nomenclature of belemnoid species important for the zonation of the European Maestrichtian (Kongiel, 1962, p. 23; Birkelund, 1965, p. 153), the diversity of proposed zonations, and the overlapping range zones of many belemnoid species (Kongiel, 1962, tables 6, 7; Birkelund, 1957, table 4) raise doubt as to the validity of the standard zonation and proposed correlations between sections (see also Wood, 1967), and are perhaps responsible for the difficulties encountered in deciding the position of the Campanian-Maestrichtian boundary (Birkelund, 1957) and of boundaries within the Maestrichtian (Ebensberger, 1962, p. 9). As most workers have employed a fourfold subdivision of the Maestrichtian, it is here accepted as a framework to which can be related the ranges of the European species of the *Tenuipteria tegulata* species group.

The stratigraphic range of the species of *Tenuipteria* in important areas is given in Figure 1. For four reasons this table should be interpreted with caution:

Firstly, *caucasica* Dobrov is treated as distinct from *tegulata* Hagenow, although future systematic work may show them to be conspecific.

Secondly, in the absence of illustrations the specific status of specimens listed as *tegulata* by many authors is uncertain. These records are treated as *tegulata* (sensu lato) but may include equivalved *tegulata* or *caucasica* and/or the inequivalved *dobrovi*.

Thirdly, the belemnoid zones of Northwest Europe and Russia are taken as approximately time equivalent. This is probably only partly true, for in Russia Jeletzky (1958; 1962, p. 1013) considers the zone of *Belemnella kasimirovensis* to include some of the "latest lower Maestrichtian" and the zone of *Belemnella lanceolata* to extend down into the uppermost Campanian.



[illegible]

Fourthly, in relating the threefold belemnoid zonation of the Lower Maestrichtian to the twofold zonation, the zone of *B. lanceolata* is taken to be equivalent to the Lower Lower Maestrichtian and the other two zones to the Upper Lower Maestrichtian. This does not correspond to the proportions shown by Jeletzky in tables accompanying his papers of 1958, 1960 and 1962.

Figure 1 suggests three patterns:

1. In both Northwest Europe and Russia older equivalved species (*tegulata-caucasica*; upper Campanian to lowermost Upper Maestrichtian) are followed by a younger inequivalved species (*dobrovi*; Upper Maestrichtian).

2. The equivalved species appears earlier in Russia (*caucasica*), in the zone of *Bostrychoceras polyplocum* (Maslakova, 1959), than in Europe (*tegulata*; Seitz, 1959), whereas the inequivalved species appears to have similar stratigraphic ranges in both regions.

3. The equivalved *tegulata* may extend into younger rocks in Northwest Europe than the equivalent *caucasica* in Russia, where *caucasica* probably did not continue to the top of the Lower Maestrichtian (Jeletzky, 1960, p. 1013; Dobrov and Pavlova, 1959). However, it should be noted that Dobrov (1951) originally recorded *caucasica* in the uppermost Lower Maestrichtian (Mst. i<sub>2</sub>) and lowermost Upper Maestrichtian (Mst. s<sub>1</sub>).

Dr. Friedrich Schmid (letter of September 27, 1966) has recently collected a poorly preserved specimen identified as *I. tegulatus* from the beds outcropping at Hemmoor at some 50 to 60 meters above the "Tonband" (Schmid, 1955, fig. 1). If the specimen is an equivalved *tegulata* Hagenow, this discovery represents a significant increase in the upward stratigraphic range of the species and places it well within the lower Upper Maestrichtian zone of *Belemnitella junior*.

If further systematic and biostratigraphic studies support these patterns, then the equivalved species (as *caucasica*) may have evolved on the Russian Platform, spreading later to Northwest Europe, and possibly becoming morphologically distinct (as *tegulata*) in the process. In this case the inequivalved *dobrovi* possibly also evolved on the Russian Platform but spread more rapidly to Northwest Europe.

FIG. 1. Stratigraphic distribution of the species of the *Tenuipteria tegulata* species group in the Upper Cretaceous of Europe. Note: *T. tegulata* (sensu lato) may include equivalved (*tegulata*, *caucasica*) and/or the inequivalved (*dobrovi*) species.

## NORTH AMERICA

In North America species of *Tenuipteria* are recorded from the Maestrichtian of the Gulf Coast and the Western Interior of the United States and Canada. Until recently the epicontinental uppermost Cretaceous sea of the Western Interior was considered to open to the south (and doubtfully to the north) (Reeside, 1957; Hattin, 1967). Gill and Cobban (1966) and Birkelund (1965, fig. 125) have shown that the sea also opened to the north into the boreal ocean.

Two faunal provinces can be recognized. There is a Western Interior province, including central Canada, with faunas dominated by baculitid and scaphitid ammonoids and bivalves; this province has affinities with the Boreal Province (Birkelund, 1965). And there is a Gulf Coast province with faunas characterized by different families and species of bivalves, a more diverse gastropod fauna (Sohl, 1964) and sparse cephalopods. Because of the incomplete systematic coverage of phyla in one or both regions, documentation of the definitive characteristics of the provinces is at present inadequate.

Biostratigraphic zonation of the upper Campanian and Maestrichtian of the Western Interior is based principally on baculitid and scaphitid ammonoids (Cobban and Reeside, 1952; Jeletzky, 1962; Gill and Cobban, 1966), although zonation of the upper part of the section equivalent to the Fox Hills Formation is hampered by a lack of systematic work on the scaphite ammonoids (Waage, 1968). The Gulf Coast sequence is zoned at a grosser level by oysters (Sohl and Kauffman, 1964), gastropods (Sohl, 1960, 1964), and other molluscs (Stephenson et al., 1942). Cephalopods are uncommon and of limited importance. Zonation of the Western Interior and Gulf Coast sequences is complicated by the occurrence of nonmarine beds at the top of the Cretaceous and by stratigraphic breaks, respectively. Consequently, the range of species and zones based on marine organisms is likely to be incomplete.

Correlation of North American sequences is given in Figure 2. Correlation between the Western Interior and the Gulf Coast is complicated by a paucity of common taxa (Waage, 1968) and depends largely on the work of Jeletzky (1960), who argues that the *Scaphites* (*Discoscaphites*) *nebrascensis* zone of Fox Hills Formation in its type area is approximately isochronous with the *S. (D.) conradi* zone of the Prairie Bluff Chalk. Because of the close similarity of their



faunas, correlation between the Western Interior and south-central Canada is good.

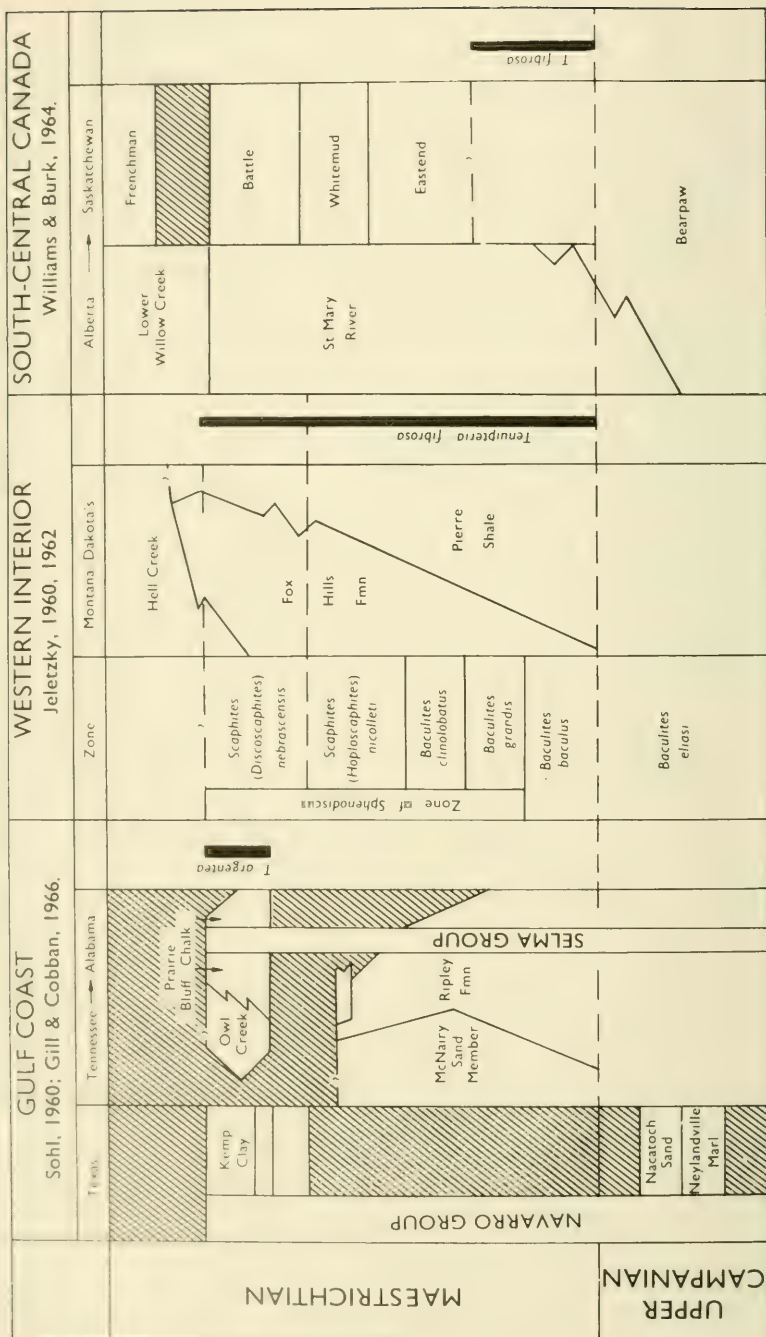
Figure 2 also shows the stratigraphic range of the North American species of *Tenuipteria*. The short range zone of *T. fibrosa* in south-central Canada is undoubtedly due to the change from marine to nonmarine deposition.

*Tenuipteria argentea* is known only from the Owl Creek and Prairie Bluff formations of northern Mississippi and southeastern Missouri. As these formations have unconformable lower and upper limits, the stratigraphic range of the species may have been much longer, a view supported by Sohl (1964, p. 155) who considers that a "moderate part of the Maestrichtian is missing." No radially ribbed, equivalved, mytiloid-shaped *Inoceramus* with relatively weak plicae which resembles *T. fibrosa* has been reported from the older units of the Navarro Group. A large subcircular right valve from the Nacatoch Sand, recorded as "*I. vanuxemi* Meek & Hayden?" by Stephenson (1941, Pl. 13, fig. 3), has strong, widely spaced, narrow concentric plicae, and fine, weak radial plicae. As the left valve holotype (Meek, 1876, Pl. 14, figs. 2a,b) and right valves studied by Meek (1876, p. 57) lack radial plicae, Stephenson's specimen should be reevaluated.

In contrast to the situation in Europe, no succession of an equivalved species followed by an inequivalved species has been recognized in any one region of North America. This may be largely due to the incompleteness of sequences and the onset of nonmarine deposition. If, as proposed by Jeletzky (1960), the Fox Hills Formation in its type area and the Prairie Bluff Chalk are correlatives, then *argentea* and *fibrosa* could have overlapping ranges much as *tegulata* and *dobrovi* overlap in the lower part of the Upper Maestrichtian *Belemnitella junior* zone of Northwest Europe (fig. 1).

#### CORRELATION BETWEEN THE LATEST CRETACEOUS OF EUROPE AND NORTH AMERICA

Correlations between the latest Cretaceous sequences of Europe and North America have been based on scaphitid and sphenodiscid ammonoids, belemnoids, and the bivalve genus "*Inoceramus*" (Seitz, 1959; Jeletzky, 1960, 1962; Birkelund, 1965; Waage, 1968). Only Cobban and Reeside (1952) and Jeletzky (1960, 1962) have proposed correlations at the intrastage level.



Cobban and Reeside (1952, p. 1026) did not document their statement that "the Fox Hills fauna corresponds to the upper Maestrichtian fauna of the European sequence". They seem to have accepted the correlation given by Stephenson and Reeside (1938, fig. 3). Jeletzky argued that the *S. (Discoscaphites) nebrascensis* zone of the type Fox Hills Formation and its equivalents in Texas and northern Mexico are Upper Lower Maestrichtian (upper part of the *Belemnella cimbrica* zone) (1960, fig. 2), and the *Triceratops* beds are of late Maestrichtian age (equal to part or all of the *Belemnitella junior* and *Belemnella kasimirovensis* zones of northern Europe). The possibility of a basal Upper Maestrichtian age for the uppermost marine Cretaceous of the Western Interior was not excluded by Jeletzky. In fact, in his text-figures (1962, text-figs. 1, 2) he extended the youngest Fox Hills Formation well into the range zone of *Belemnitella junior* (lower Upper Maestrichtian).

Considerable doubt exists as to the position of the base of the Maestrichtian Stage in the Western Interior sequences. Most workers follow Jeletzky (in Cobban and Reeside, 1952, p. 1026–1027) in tentatively placing the lower boundary of the stage at the base of the zone of *Baculites baculus*. On the evidence of the ammonites the boundary could be placed either at the base of the *B. baculus* zone or possibly within or at the top of the zone. Jeletzky favored the first alternative, emphasizing the appearance of certain European Lower Maestrichtian scaphitid species even though late Campanian European species are also present in the zone of *B. baculus* and other typical European Lower Maestrichtian species appear high in or above the *B. baculus* zone. Doubt about the stratigraphic ranges of many of the North American ammonoid species, and lack of documentation that the North American and European species discussed by Jeletzky are conspecific (Birkelund, 1965; Waage, 1968) increase the uncertainties of the proposed correlations between the regions.

Similarly, the position of the boundary between the Lower and Upper Maestrichtian in the Western Interior is uncertain. Most workers accept Jeletzky's (1962, p. 1008) selection of the upper limit as the top of the range zone of *Discoscaphites nebrascensis*.

Jeletzky (1960, 1962) placed a lot of weight for an upper Lower Maestrichtian age for the type Fox Hills Formation on his discovery

FIG. 2. Stratigraphic distribution of the species of the *Tenuipteria tegulata* species group in the Upper Cretaceous of North America.



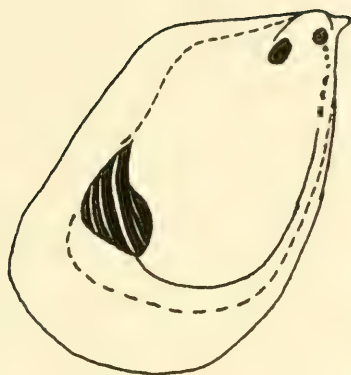
at Hemmoor of an ammonoid fragment which he identified as *S. (H.) nicolleti*. Both Birkelund (1965) and Waage (1968) consider the fragment indeterminable. Waage goes further in showing it to be morphologically distinct from the true *nicolleti* of the Western Interior. After an analysis of the belemnoids, scaphitids and spenodiscids, Waage concludes that an inadequate knowledge of the systematics, biostratigraphy, paleoecology and paleogeography of these taxa in both Europe and North America prevents refined correlations between the two regions. Of the cephalopods he emphasizes the potential value of hoploscaphitid ammonoids for correlation at the intrastage level (see also Birkelund, 1966).

The stratigraphic distribution of the species of *Tenuipteria* in Europe and North America tends to support Jeletzky's correlations. The equivalved species appear about the same time, latest Campanian, in both regions—at least in Russia and south-central Canada if the specimen of *fibrosa* from some 80 feet below the Belanger Sandstone Member of the Bearpaw Formation (Furnival, 1946, p. 62), and hence probably below the zone of *Baculites baculus*, is correctly identified. The absence of an inequivalved species of *Tenuipteria* in the Western Interior of the United States and Canada, together with the lack of other index taxa, counts against the presence of Upper Maestrichtian marine beds. Likewise, the occurrence of the inequivalved *T. argentea* in the Prairie Bluff Chalk of the Gulf Coast is compatible with a correlation with the latest Lower Maestrichtian and earliest Upper Maestrichtian.

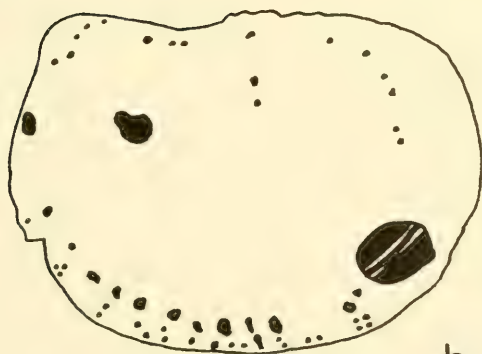
However, the present inadequate knowledge of the systematics, biostratigraphy and paleogeography of the species of *Tenuipteria*, coupled with the uncertain status of European latest Cretaceous biostratigraphy, negates the possibility of precise correlations. Theoretically, the species need not have isochronous range zones in Europe

FIG. 3. Muscle scar and pallial line impressions for inoceramid species from the uppermost Cretaceous of the Western Interior of the United States.

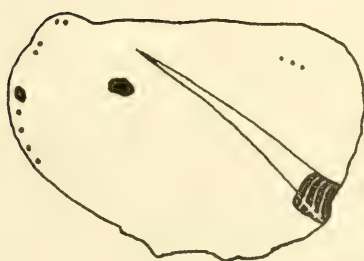
- 3a. *Tenuipteria fibrosa* (Meek and Hayden). YPM 24037, drawn from the original of Plate 1, figure 5. The dashed line indicates the position of edge of the inner shell layer.
- 3b. "*Inoceramus*" *barabini* Morton. YPM 24052, Pierre Shale, Converse County, Wyoming, C. E. Beecher and J. B. Hatcher, collectors.
- 3c. "*Endocosta*" *typica* Whitfield. YPM 24053, Pierre Shale, Converse County, Wyoming.



a



b



c

and North America. Assuming that *caucasica* and *tegulatus* are conspecific, and that the correlations are correct, the nonisochroneity of some range zones would be well documented by the appearance of *caucasica* in Russia before the entry of *tegulatus* in Western Europe—a difference equivalent to the range zone of *Belemnitella lanceolata* (Fig. 1). Even if species are able to spread geographically in a geologically insignificant time interval, the evolution of a species in a region may involve at least half a million years (Gill and Cobban, 1966), and the migration and establishment of a species may be prevented by environmental, biological (Briggs, 1967), geological or hydrographic factors. For example, the later appearance of an equivalved species of *Tenuipteria* in Western Europe may be due largely to environmental control. Until detailed systematic and biostratigraphic studies are completed these arguments tend to be semantic.

Possibly the best evidence for the correlation of the Western Interior sequence comes from the assessment of biostratigraphy and potassium-argon ages prepared by Gill and Cobban (1966, p. 34–37). These authors demonstrate that the base of the *Baculites baculus* Range Zone, which is correlated with the base of the Lower Maestrichtian, is at about 70 million years, and that the *Discoscaphites nebrascensis* Range Zone is older than  $66 \pm 2$  million years and estimated to be about 68 million years. Although these dates give a reasonably good fix for the Western Interior sequence and tend to place the youngest marine Cretaceous of the Western Interior in the latest Lower Maestrichtian, correlation with the European stages remains dependent on classical biostratigraphic methods. Refined correlation is not possible until radiometric ages are available for European sequences.

#### SYSTEMATIC DESCRIPTIONS

##### *Tenuipteria* Stephenson 1955 Emend.

##### SYNONYMY.

*Tardinacera* Elias, 1931, opp. p. 58, p. 122, 130 (nomen nudum).  
*Spyridoceras* Heinz, 1932, p. 19 (invalid, no diagnosis).

TYPE SPECIES. By original designation of Stephenson (1955, p. 110),



*Inoceramus argenteus* Conrad (1958, p. 329), Owl Creek Formation, Maestrichtian, Gulf Coast, North America.

DIAGNOSIS. Thin-shelled inoceramid characterized by radial and concentric plicae, a distinct small anterior auricle and a narrow ligament area, concave in cross section, longitudinally striated, either lacking ligament pits (*fibrosa*, the stratigraphically younger *tegulata*) or with faint, broad, irregular, weakly impressed pits (stratigraphically older *tegulata*, *argentea*). Muscle scars consist of a posteroventrally situated large adductor scar and two anterodorsal byssal-pedal scars which are joined by a pallial line of discrete scars anterodorsally but fused ventrally (*fibrosa*).

EMENDED DESCRIPTION. Equivalved or inequivalved, when the left valve is the more strongly inflated, small to medium sized with a distinct anterior ear, usually delimited from the main disc of the shell, and a flattened, rounded, posterior dorsal margin. Umbones anterior, moderately projecting on equivalved species, strongly projecting on the left valve but only slightly projecting on the right valve of inequivalved species. Shell ornamented by radial and concentric plicae of variable strength and numbers, usually regular and tending to produce a distinctive "tile-like" pattern, but sometimes with the radial plicae stronger than the concentric, or vice versa. Along the crest and ventral flank of the concentric plicae are concentric lamellae which are dominant on the posterodorsal flank where the plicae are subdued or absent. Shell thin, of two layers: a thicker, outer prismatic shell layer which may project well beyond the margin of a thinner, inner nacreous shell layer (*fibrosa*, *tegulata*).

DISCUSSION. The above diagnosis has been made broad to include species of similar external ornament and shape, but either equivalved or inequivalved, and having a range of ligament area and musculature characteristics. In the diagnosis and description species names in parentheses are given after those features where the morphology is known from less than three species.

Species included in my broad concept of *Tenuipteria* are

*Tenuipteria tegulata* (Hagenow, 1842)

*T. fibrosa* (Meek and Hayden, 1856a)

*T. ? caucasica* (Dobrov, 1951)

*T. argentea* (Conrad, 1858)

*T. ? dobrovi* (Jeletzky and Clemens, 1965)

As discussed above, *fibrosa* and *caucasica* might be conspecific with *tegulata* and *dobrovi* with *argentea*. Because of lack of knowledge of the morphology of their ligament areas, *caucasica* and *dobrovi* are tentatively classed in the genus.

All species included in *Tenuipteria* differ from *Inoceramus* in one or a combination of the internal morphological characteristics.

Future work may show that the equivalved species with a few very weak or no ligament pits and a partly continuous pallial line (*Tenuipteria tegulata*, *fibrosa*, ?*caucasica*) should be separated subgenerically or generically from the inequivalved species with irregular, weak ligament pits, strongly inflated umbone and the correlated smaller anterior ear and convex anterodorsal margin on the left valve (*argentea*, ?*dobrovi*).

The Turonian genus *Didymotis* Gerhardt (1897) has a smooth ligament area lacking pits (Imlay, 1955) and superficially resembles *Tenuipteria* in shape, ornament and possession of a thin shell. However, the equivalved species of *Didymotis* are oval in shape, have inconspicuous subcentral umbones and a long, straight dorsal margin, and lack the distinctive regular "tile-like" ornament of *Tenuipteria*. On *Didymotis* irregular, closely spaced, concentric plicae dominate the few weak, widely spaced, radial plicae that occur only on the main disc of each valve (Gerhardt, 1897, Pl. 5, figs. 3a,b). The morphological differences between the genera, and the reasonable assumption of derivation from different inoceramid stocks at different times warrant their treatment as separate taxa. The resemblance of *Didymotis* to *Tenuipteria* is undoubtedly due to convergence, perhaps dependent on the adoption of a similar mode of life.

### *Tenuipteria fibrosa* (Meek and Hayden)

(Plate 1, figs. 1–6; Fig. 3a)

*Avicula?* *fibrosa* Meek and Hayden, 1856a, p. 86–87.

*Pholadomya fibrosa* (Meek and Hayden). Meek and Hayden, 1856b, p. 283.

*Pinna fibrosa* (Meek and Hayden). Meek, 1864, p. 9.

*Avicula* (*Pseudoptera*) *fibrosa* (Meek and Hayden). Meek, 1873, p. 489.

*Pteria* (*Pseudoptera*) *fibrosa* (Meek and Hayden). Meek, 1876, p.

36–37, Pl. 17, figs. 17a–d. Whitfield, 1880, p. 386, Pl. 7, fig. 5. Whiteaves, 1885, p. 32, Pl. 4, fig. 1.

*Inoceramus (Actinoceramus) whitii* Toepelman, 1922, p. 63.

*Inoceramus (Actinoceramus) fibrosus* (Meek and Hayden). Dobbin and Reeside, 1929, p. 20.

*Tardinacara (Pseudoptera) fibrosa* (Meek and Hayden). Elias, 1931, opp. p. 58, p. 124, p. 130. Searight, 1934, p. 4.

*Inoceramus (Actinoceramus) fibrosa* (Meek and Hayden). Russell, 1940, p. 88.

*Inoceramus fibrosus* (Meek and Hayden). Landes, 1940, p. 136–137. Cobban and Reeside, 1952, p. 1020, and correlation chart. Jeletzky, 1962, p. 1011–1014, Pl. 141, figs. 4–7. Seitz, 1959, p. 123–124 (? synonymous with *I. tegulatus* Hagenow (1842, p. 559)).

*Inoceramus radiatus* Kellum, 1962, p. 57, Pl. 5, fig. 17 (*non* Heine, 1929, p. 105, Pl. 18, figs. 68, 69).

*Inoceramus cobbani* Kellum, 1964, p. 1006 (new name for *I. radiatus* Kellum).

*Inoceramus? tegulatus* Hagenow, 1842 (*non* Ødum, 1922). Jeletzky, in Jeletzky and Clemens, 1965, p. 957.

*Tenuipteria fibrosa* (Meek and Hayden). Speden, 1970, Pl. 8, figs. 11–18; Pl. 9, figs. 1–16.

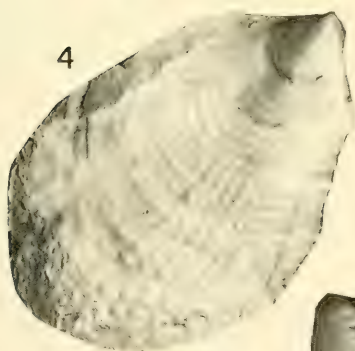
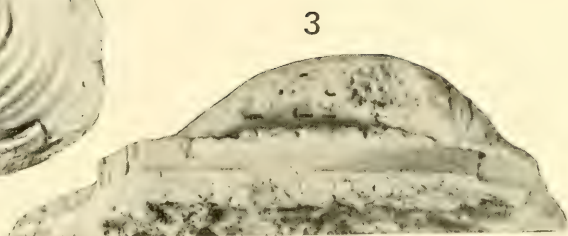
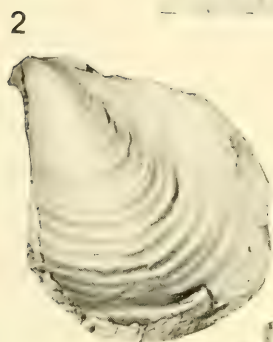
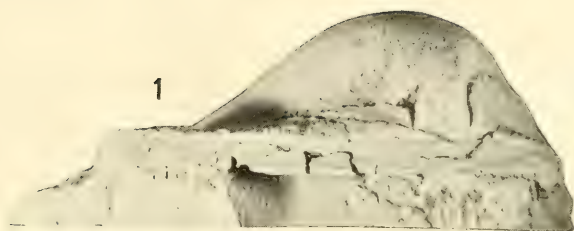
DESCRIPTION. Specimens 5 to 55 mm long, equivalved, inequilateral, maximum inflation about mid-height close to anterior margin. Shape extremely variable, submytiloid to subquadrangular, and rarely almost oval. Height, anterior length and width are, respectively, 83 to 100, 8 to 15 and 12 to 27 percent of the length of the outline of the inner shell layer. Dorsal margin straight, posterodorsal margin rounded, and the angle subtended at the umbone by the dorsal margin and the line joining the posteroventral extremity is about 40 to 50 degrees. Umbones prosogyrous, sited near the anterior end of the straight dorsal margin, not prominent, project only slightly above the dorsal margin. Anterior auricle distinct, always present, relatively small but of variable size, delimited from the moderately to strongly inflexed anterodorsal margin by a narrow groove of variable prominence. When the anterodorsal margin is strongly inturned the associated groove is deep, and there is a distinct byssal notch and gape where the groove meets the margin. Otherwise, the byssal notch and gape are small or indefinite.



## PLATE 1

*Tenuipteria fibrosa* (Meek and Hayden)

1. YPM 24644; ligament area of a left valve. Note the lack of ligament pits. YPM A-1140, Locality 115, *Protocardia-Oxytoma* Assemblage Zone, Little Eagle lithofacies, Trail City Member, Fox Hills Formation. X1.5.
- 2.3. YPM 24033; the divergence of the outer prismatic layer from the inner layer dorsally and strong concentric plicae (2), and the striated ligament area which lacks ligament pits. YPM A-992, Locality 231, Lower *nicolleti* Assemblage Zone, Little Eagle lithofacies, Trail City Member, Fox Hills Formation. Fig. 2 X1, Fig. 3 X2.
4. YPM 24039; right valve steinkern with equally strong radial and concentric plicae. YPM A-336, Locality 32, Mobridge Member, Pierre Shale. X1.
5. YPM 24037; right valve steinkern with a posteroventrally situated adductor scar and two anterior byssal-pedal scars on either side of an umbonal fracture. The specimen on which Figure 3a is based. YPM A-350, Locality 39, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation. X6.
6. YPM 24028; left valve steinkern with strong radial plicae. YPM A-336, Locality 32, Mobridge Member, Pierre Shale. X2.



Ornament extremely variable, consisting of concentric and radial plicae usually of equal size and regular and giving a distinctive "tile-like" pattern, but sometimes with stronger radial or concentric plicae. Radial plicae appear at about 5 to 20 mm from the tip of the umbone and are absent only rarely on specimens longer than 20 mm. Radial plicae absent from the posterodorsal flank of the valve where the concentric plicae also weaken and concentric lamellae dominate. A concentric lamella occurs along the crest or along the dorsal part of the ventral flank of each concentric plica. Specimens greater than 30 mm in height have about 15 to 30 radial plicae, which are usually slightly wider than the interspaces, and about 20 to 35 concentric plicae. Some specimens have irregular broad undulations bearing three to four of the regular concentric plicae.

Ligament area extends the length of the dorsal margin, inclined at 30 to 40 degrees to the commissural plane, generally strong concave and almost semicircular in cross-section, or more rarely L-shaped with a wider, slightly concave dorsal limb and a flat ventral limb inclined at 60 to 80 degrees to the commissural plane. Surface of ligament area marked by fine longitudinal striae separated by much wider shallow grooves; striae stronger on the dorsal part of the ligament area, often weak or absent on the ventral part. Ligament area lacks impressed pits, but rare specimens show traces of faint shallow undulations. In the vicinity of the umbones the dorsal margin usually strongly overhangs the ligament area.

Posterior adductor scar large, elliptical to pear-shaped, tapering posterodorsally where deeply impressed at extremity, anterior margin with an indentation of variable prominence, situated at postero-ventral extremity of inner shell layer close to its junction with outer shell layer; rarely preserved. In the umbonal cavity are two antero-dorsal scars (pedal-byssal retractors), a small oval impression anterior to the line of maximum inflation and a slightly larger subrectangular scar posterior to the line of maximum inflation. Pallial line on inner shell layer close to junction with outer shell layer, consisting of a narrow continuous band with irregularly spaced swellings from the posterior adductor to above mid-height of shell, then continuing as a series of four to eight small discrete oval or linear impressions. Above the anterior pedal-byssal scar and close to the dorsal margin are sometimes seen three to five scars.

Calcitracum very thin and fragile, observed maximum thickness 0.7 mm, rarely exceeds 0.5 mm, composed of a thick, outer prismatic



layer and a thin, inner pearly nacreous layer one quarter to one sixth of the thickness of the outer layer. Outer layer extends considerably beyond the inner layer, forming a broad flange. Internal surface of the umbonal cavity is marked by fine irregular striae which approximately parallel the growth axis. Many specimens have a faint ridge along a line extending from the dorsal margin posterior to the umbone to the anterodorsal end of the posterior adductor.

TYPE SPECIMEN. Lectotype of *Avicula? fibrosa* Meek and Hayden, by subsequent designation of Meek (1876, Pl. 17, fig. 17a), USNM 460, a steinkern of a right valve, oblique length 34.7 mm. Type locality: Forks of the Cheyenne River, South Dakota. Stratigraphic position: Pierre Shale, Early Maestrichtian, Upper Cretaceous.

OCCURRENCE. In the Western Interior of the United States *T. fibrosa* occurs in the Pierre Shale and Fox Hills Formation and ranges from the *Baculites baculus* zone through to the top of the Timber Lake Member of the Fox Hills Formation. In the type area of the Fox Hills Formation it is common only in the Lower and Upper *nicolleti* assemblage zones (Waage, 1961). In south-central Canada it is known only from the upper part of the Bearpaw Formation (Jeletzky, 1962, p. 1012; and see Furnival, 1946, p. 62).

DISCUSSION. The description given above is based on specimens from the Mobridge Member, Pierre Shale, and the Fox Hills Formation in its type area. The reader is referred to Speden (1970) for additional illustrations of specimens of *fibrosa* and data on occurrence. No account is taken of the morphological variation described for other samples by Cobban (1964).

Important features of the morphology of *T. fibrosa* are discussed below:

a) *Shape*. The variation in shape is marked. A striking feature of complete specimens is that the outline of the outer shell layer does not parallel the outline of the inner shell layer. This divergence is most marked along the posterior and posteroventral margins, while the dorsal margin of the ligament area diverges from the dorsal margin of the inner shell layer by angles of 10 to 25 degrees (Pl. 1, fig. 2). The outline of steinkerns is usually defined by the margin of the inner shell layer, and all too frequently the thin outer shell layer breaks off along its junction with the inner layer. Consequently, the

shape based on steinkerns, or even shelled specimens, may be false. *Tenuipteria fibrosa* tends to be more oval than is indicated by the typical mytiloid steinkerns.

Because of the wide variation in shape shown by *fibrosa*, and the nonparallelism of the outlines of the outer and inner shell layers, only gross measurements are given in the above description.

b) *Ornament*. The Fox Hills "populations" are characterized by extremely variable ornament. Normally, the radial and concentric plicae are of almost equal strength, although the concentric ornament is commonly stronger than the finer and more regular radial plicae. Specimens with strong radial sulci, which closely resemble the lectotype, are present in many collections from all assemblage zones but are more common in the Mobridge Member of the Pierre Shale along the Moreau River (YPM A-336). The radial plicae are very weak on some small specimens, particularly those in collections from the Timber Lake Member, Fox Hills Formation. However, this weakness may be related to the factor of size.

The pattern of ornament shown by the Fox Hills "populations" covers the third and fourth "forms" of Cobban (1964, i.e. those with "concentric and radial sculpture . . . of about equal strength, and a final form in which the concentric sculpture dominates". It should be stressed that the individual specimens may have very strong or very weak radial plicae. The range of variation of ornament in a single collection at a locality prevents positive placing in either of Cobban's "forms", at least until they are more fully documented.

Ornament studies ideally should be based on external moulds or the original shell surface and not on steinkerns, which are often all that a paleontologist has to study. In the case of the Fox Hills samples the narrow radial plicae are notably more subdued on the steinkern than on the external mould or shell surface

c) *Ligament area*. The ligament area is basically smooth and lacks the incised, transverse, rectangular ligament pits characteristic of the genus *Inoceramus*. Rare specimens show traces of faint shallow undulations on the floor of the ligament area. These, however, are irregular and cannot be compared with the ligament pits of *Inoceramus*. Odum (1922) records the presence of similar faint undulations on his specimens of *T. tegulata* from the White Chalk of Denmark and shows the presence of small ligament pits on the dorsal half of the ligament area of a specimen from Møns Klint (1922, fig. 6). According to Birkelund (letter of February 2, 1966), the specimen

with ligament pits from Møens Klint is stratigraphically older than the specimens from Aalborg which lack pits.

Small but distinct pits occur on the dorsal part of the ligament area of specimens of *Inoceramus* cf. *barabini* Morton (YPM 24452, 24055), labeled as from Converse County, Wyoming, Pierre Shale (Campanian), C. E. Beecher and J. B. Hatcher, collectors, held in the Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University. On these specimens the pits are smaller and less definite toward and under the umbones (Speden, 1970). Derivation of the *fibrosa* type of pitless ligament area by degeneration from a typical *Inoceramus* ligament area with pits is suggested by these observations.

d) *Musculature*. Musculature is rarely described for species of *Inoceramus*, largely because of the lack of impression of the scars into the thin shell and the poor preservation of specimens. The adductor scar of *fibrosa* is also hard to find for the above reasons, and also because it is sited so close to the posteroventral margin of the inner shell layer, a portion of the shell often broken or not collected.

A search of the literature indicates that the musculature of species classed in *Inoceramus* consists characteristically of a pallial line of discrete scars and a posterior adductor scar sited in a submedial position (see Jones and Gryc, 1960, p. 159). Kauffman (1965) has recently recognized three types of muscle scar patterns in Cretaceous species of *Inoceramus*. One category includes that of *T. fibrosa* as described above. Other Upper Cretaceous "*Inoceramus*" species have a musculature pattern similar to that of *fibrosa*, but with a pallial line consisting solely of discrete scars and generally with small scars extending in a line across the posterodorsal part of the shell. A specimen (YPM 24052) of the "*Inoceramus*" *barabini* complex and two specimens (YPM 24053) labeled "*Endocostea typica* Whitf.", all from "Converse County, Wyoming, Pierre Shale", C. E. Beecher and J. B. Hatcher, collectors, have this type of pattern (Figs. 3b,c; see also Speden, 1970).

Species of recent isognomiid genera (*Isognomon*, *Melina*) have a very similar pattern of muscle scars, with two small byssal-pedal scars in an anterodorsal position, but the large adductor scar is usually in a more subcentral position on the inner shell layer and is joined to the anterior of the two anterodorsal scars by a line of discrete small pallial scars. The possession of similar musculature patterns supports the close relationship between the isognomiid and



inoceramid stocks postulated on stratigraphic and other morphological grounds by many workers (Cox, 1940; Hayami, 1960). In the case of *fibrosa* the resemblance is probably secondary and due to convergence through the adoption by an inoceramid stock of an epi-faunal mode of life similar to that of *Isognomon*.

COMPARISONS. Seitz (1959) suspected that *T. tegulata* Hagenow (not of Ødum) might be synonymous with *T. caucasica* Dobrov and *T. fibrosa* Meek and Hayden, but he stressed the need for further study of better preserved and more abundant specimens before his proposed synonymies could be accepted as valid. Jeletzky (1962), using the concept of *tegulata* Hagenow as an inequivalved species, synonymized *caucasica* Dobrov with *fibrosa* Meek and Hayden. In 1965 Jeletzky (Jeletzky and Clemens, 1965) accepted *tegulata* Hagenow as being an equivalved, morphologically variable species and synonymized *fibrosa* and *caucasica* under *tegulata* Hagenow.

Seitz considered that *T. fibrosa* differs from *T. tegulata* Hagenow in having growth lamellae which are convex ventrally across the raised nodular radial plicae, whereas they are convex dorsally on *T. tegulata*. On specimens of *fibrosa* from the Fox Hills Formation, South Dakota, the growth lamellae and striae may be concave or convex dorsally across the raised radial plicae, and an individual lamella may have both orientations along its length. On most specimens the second order concentric costate ornament has a straight or slightly convex ventral trace. Only on specimens where a very nodular pattern is produced by strong radial and concentric plicae do the lamellae have a convex dorsal trace. The growth lamellae on specimens of *T. dobrovi* available to me have an irregular trace, while a specimen of *T. tegulata* (the original of Ødum, 1922, fig. 5) does not show clearly the concentric lamellate ornament across the radial plicae on the main disc of the valve. On the posterodorsal flank the lamellae are irregularly undulating. Although the difference between *tegulata* Hagenow and *fibrosa* noted by Seitz is unlikely to be of specific rank, additional data on the consistency of orientation of the trace of these lamellae across the radial plicae are required to confirm my opinion.

The few specimens and illustrations of *tegulata* Hagenow and *caucasica* available to the writer indicate, as suggested by Seitz (1959) and Jeletzky and Clemens (1965), that the three equivalved species *tegulata*, *fibrosa* and *caucasica* might be synonymous. The three "species" include forms with a wide variation of shape and

similar ornament. Specimens of *fibrosa* greater than 30 mm in height have about 15 to 30 radial raised plicae and about 20 to 35 concentric plicae (see p. 28). Ødum's (1922, fig. 5) specimen of *tegulata* Hagenow has an indefinite number of radial plicae and about 25 concentric plicae, while those of *caucasica* figured by Dobrov (1951) have about 10 to 30 radial and 20 to 35 concentric plicae.

Cobban (1964), in his recognition of his ornament groups, has emphasized the variation in strength of radial and concentric plicae.

Our present knowledge is insufficient to permit the synonymizing of the three species. Detailed studies are required of the stratigraphic and biogeographic variation of adequate samples of the European species such as are being undertaken by Cobban (1964) for the North American *T. fibrosa*.

*Tenuipteria argentea* (Conrad)

(Plate 2, fig. 7; Plate 3, figs. 1-6)

*Inoceramus argenteus* Conrad, 1858, p. 329, Pl. 34, fig. 16.

*Inoceramus costellatus* Conrad, 1858, p. 329, Pl. 34, fig. 12.

*Inoceramus argenteus* Conrad. Stephenson and Monroe, 1940, p. 280, Pl. 10, figs. 8, 9.

*Tenuipteria argentea* (Conrad). Stephenson, 1955, p. 111, Pl. 16, figs. 4-9.

REDESCRIPTOR. Species of moderate size, specimens from about 10 to 65 mm long, inequilateral, inequivalved, umbones prosogyrous.

Right valve slightly to moderately inflated, the umbone barely projecting above the dorsal margin, the anterior auricle small and distinct. Left valve strongly inflated with a prominent umbone projecting above the dorsal margin, anterior auricle small. Posterodorsal margin of each valve rounded.

Valves ornamented by radial plicae, strongest on the right valve, which divide by gemmation on the center of the disc, become wider ventrally and are separated by narrower interspaces. Radial plicae number about 25 to 30 on the left valve ( $N = 4$ ) and 26 to 33 on the right valve ( $N = 4$ ). Posterodorsal third of the shell and the antero-dorsal margin lack radial plicae. Radial plicae crossed by regular weak concentric plicae which are accentuated by a prominent growth

## PLATE 2

*Tenuipteria tegulata* (Hagenow)

- 1, 2, 3. MMH 1816; the original of Ødum, 1922, fig. 5, a left valve steinkern with shell dorsally showing anterior ear, slightly projecting umbone, and a longitudinally striated ligament area which lacks ligament pits. Aalborg, Lower Maestrichtian. (Plaster cast NZGS-WM 8956). Figs. 1, 2 X3; Fig. 3 X1.

*Tenuipteria dobrovi* (Jeletzky)

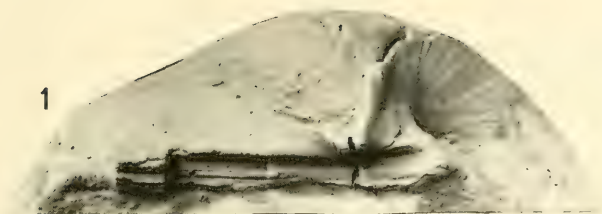
4. MMH 1814; poorly preserved left valve, the original of Ødum, 1922, figs. 1, 2. "Dania" at Mariager, Upper Maestrichtian. (Plastic cast NZGS-WM 8957). X1.
5. MMH collection 1965/694; left valve steinkern. Limhamn, Scania, Sweden. Upper Maestrichtian. X1.
6. MMH collection 1965/693; left valve steinkern. Limhamn, Scania, Sweden. Upper Maestrichtian. (Plaster casts NZGS-WM 9238). X1.

*Tenuipteria argentea* (Conrad)

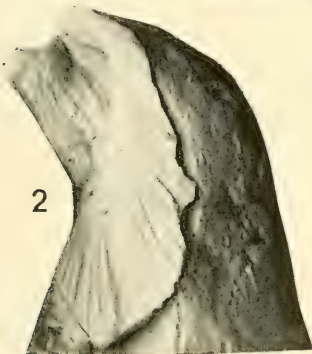
7. USNM Cat. No. 159947; left valve, incomplete. Topotype. USGS Locality 707, USNM 20661, Owl Creek, Mississippi, Maestrichtian. X2.



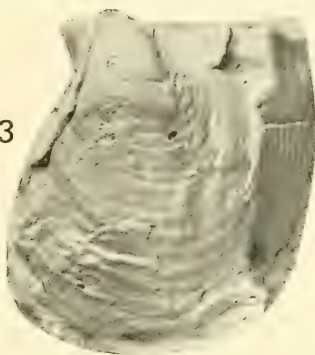
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2



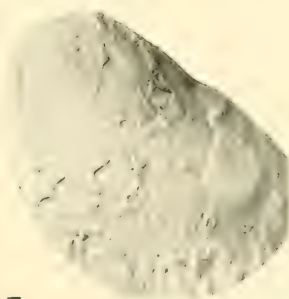
3



4

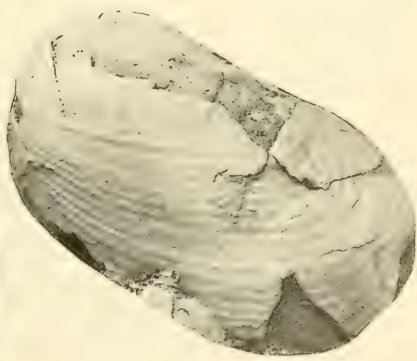


5



7

6



## PLATE 3

*Tenuipteria argentea* (Conrad)

1. USNM Cat. No. 159948; an incomplete bivalved specimen. X1.5.
2. USNM Cat. No. 159949; right valve showing lack of radial plicae on the posterior flank. X1.5.
3. USNM Cat. No. 159947; left valve ligament area showing weak ligament pits. X2.
4. USNM Cat. No. 159948; left valve of specimen of Figure 1. X1.5.
- 5, 6. USNM Cat. No. 159950; right valve showing ornament and ligament area with more strongly incised ligament pits and distinct anterior auricle. Fig. 5 X1.5; Fig. 6 X3.

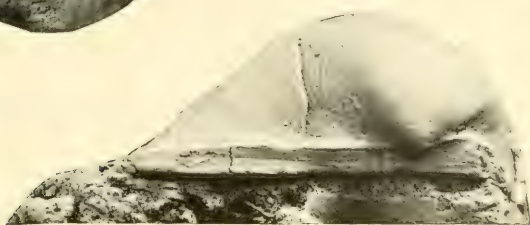
All specimens are topotypes from USGS Locality 707, USNM collection 20661, Owl Creek, Mississippi, Owl Creek Formation, Maestrichtian.



1



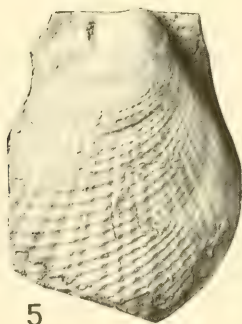
2



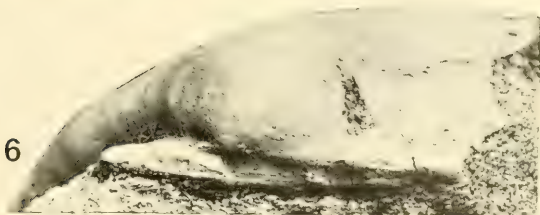
3



4



5



6

lamella developed along the crest of each plica. Concentric plicae closely spaced on umbonal 10 mm of shell, on the dorsal flanks and along the ventral margins of adult specimens, but number about one per millimeter on the main disc of the shell. The intersection of radial and concentric plicae produces a distinctive tile-like pattern of shallow rectangular depressions.

Ligament area more or less flat, bearing two to five shallow sub-rectangular or subtrigonal ligament pits; that under the umbone the largest, and sometimes consisting of two fused pits. Pits and interspaces crossed by fine striae extending the length of the ligament area. Ligament area of the right valve inclined at about 20 to 30 degrees to the plane of the commissure, and that of the left valve inclined at about 60 to 80 degrees

Muscle scars unknown. Shell very thin; shell of the main disc attaining a maximum thickness of about 0.5 mm, consisting of a thick, inner nacreous lamellar layer (0.4 mm) and a very thin, outer prismatic layer (0.1 mm).

TYPE SPECIMEN. Neotype, USNM 124102, here designated, a topotypic left valve shell showing the ligament area, the original of Plate 16, figure 6 of Stephenson (1955), USGS 6464. Type locality: Owl Creek, three miles northeast of Ripley, Tippah County, Mississippi (E  $1\frac{1}{2}$  Sec. 7, T.4 S, R.4 E). Stratigraphic position: Owl Creek Formation, Maestrichtian.

Stephenson (1955) presumed that the holotype was lost, and this was confirmed subsequently by Richards (1968). Conrad (1858) did not record the number of species he studied, but apparently no syntypes are present in the collection of the Academy of Natural Sciences, Philadelphia. Consequently, one of the topotypic specimens studied by Stephenson when he established the genus is selected as a neotype.

DISCUSSION. The above redescription is based on the examination of about 60 specimens, mostly incomplete and slightly crushed, in collections held by the United States National Museum, catalogue numbers USGS 6875 (N=6), USNM 20612 (N=22) and USNM 20661 (N=31), kindly forwarded to the writer by the courtesy of Dr. Erle G. Kauffman.

Measurements taken from the best specimens in these collections are given in Table 1. Because the measurements are based on the outline of the inner shell layer they should be accepted with caution.



TABLE 1. Measurements of specimens (in mm) of *Tenuipteria argentea* (Conrad).

No.	Valve	Length	Height	Half width	Anterior length	Length of dorsal margin	DUPM*
USNM 20661	right	17	32	7.0	4.6	—	—
"	left	29	30	14.0	3.0	18	4.5
"	left	65	62	14.0	15.0	41	—
"	left	15	13	2.0	2.5	12	—
"	right	27	26	7.0	4.0	18	—
"	right	25	25	6.0	5.0	22	—
20612	left	39	42	18.5	6.0	28	6.5
"	right	40	41	10.0	6.0	—	—
USGS 6875	right	31	28	5.0	6.0	24	—
"	right	49	45	7.0	9.0	33	—

\*Distance the umbone of the left valve projects above the dorsal margin of the ligament area.

COMPARISONS. Dobrov (1951, p. 164) was the first to suggest the presence in the latest Cretaceous of North America of the inequivalved group of "*Inoceramus tegulatus*". *Tenuipteria dobrovi* Jeletzky (1965) externally closely resembles *T. argentea* in having a strongly inflated left valve and a flattish right valve, with both valves ornamented by regular to subregular radial and concentric plicae and concentric lamellae.

Examination of specimens of *Tenuipteria argentea* in three collections held by the United States National Museum, Washington (catalogue numbers USGS 6875 and USNM 20612 and 20661), three left valves of *T. dobrovi* from the late Maestrichtian of Denmark, and illustrations indicates that the valves of these species are very similar in size and shape. Each species has left valves with height to length ratios of about one. *Tenuipteria argentea* has height to length and half width to length ratios for left valves of 0.87 to 1.14 ( $N = 5$ ) and 0.22 to 0.47 ( $N = 3$ ), respectively; for *T. dobrovi* the ratios are 1.00 to 1.20 ( $N = 3$ ) and 0.23 to 0.34 ( $N = 4$ ), respectively. Because of the inadequate numbers of specimens these values can be taken only as an indication of similarity.

On both *T. argentea* and *dobrovi* the radial plicae are most distinct on the central and anterior part of the valve and are weak or lacking on the broad posterior ear. Replicas of two left valves of *dobrovi* from the Maestrichtian of Denmark, NZGS-WM 8957 (the

original of Ødum, 1922, figs. 1, 2; height = 46 mm; Pl. 2, fig. 4) and NZGS-WM (height 43 mm; Pl. 2, fig. 6), have 17 and 23 radial plicae and about 37 and 29 concentric plicae, respectively. Photographs of a left and a right valve of *argentea* figured by Stephenson (1966, Pl. 16, figs. 4, 6) suggest the presence of about 18 radial plicae; the concentric plicae could not be counted. Topotypes of *argentea* from Owl Creek, Mississippi, in collection Cat. No. 20661 held by the U.S. National Museum, have 25 to 30 radial plicae on the left valve ( $N = 4$ ) and 26 to 33 on the right valve ( $N = 4$ ). These valves, which are 20 to 41 mm high, have about one concentric plica per millimeter on the main disc, i.e. about 25 to 45 per valve.

The close external similarity of *T. dobrovi* and *argentea* suggests that they may be conspecific and congeneric. However, the ligament area of *dobrovi* has not been described or illustrated. Until the internal morphology of *dobrovi* and the external morphology of both species are more fully known, the synonymy of the two species is uncertain though possible.

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